

Encoding binary patterns of neural activity in networks of threshold-linear neurons

Carina Curto · Anda Degeratu · Vladimir Itskov

Abstract Networks of neurons in the brain encode memories via their synaptic connections. Despite receiving considerable attention, the precise relationship between network connectivity and encoded activity patterns is still poorly understood. In particular, given a prescribed list of binary patterns, it is not generally known how to arrange the connectivity of a network so that exactly those patterns are encoded, while avoiding unwanted “spurious” states. Here we consider this problem for networks of threshold-linear neurons. We introduce a simple encoding rule that selectively turns “on” synapses between neurons that co-appear in one or more patterns. The synapses are *binary*, in the sense of having only two states (“on” or “off”), but also *graded*, with heterogeneous weights drawn from an underlying synaptic strength matrix S . Our main results provide necessary and sufficient conditions on S guaranteeing that prescribed patterns can be encoded, while maintaining tight control over spurious states. As an application, we construct networks that encode hippocampal place field codes nearly exactly. We suggest that, in this context, spurious states can be *advantageous*, allowing neural codes to be accurately encoded from a highly undersampled set of patterns. To obtain our results, we use ideas from convex and distance geometry, such as Helly’s Theorem and Cayley-Menger determinants, revealing a novel connection between these areas of mathematics and coding properties of neural networks.

Introduction

Networks of neurons in the brain encode memories via their synaptic connections. These memories are often modeled as binary patterns of neural activity associated to steady state attractors of a recurrent network [19, 2, 17]. A *binary pattern* on n neurons is a string of 0s and 1s, with a 1 for each active neuron and a 0 denoting silence; equivalently, it is a subset of (active) neurons $\sigma \subset \{1, \dots, n\}$. Given a prescribed set of binary pat-

terns, how can one arrange the connectivity structure of a recurrent network such that precisely those patterns are encoded, while minimizing the emergence of unwanted “spurious” states? This problem, which we refer to as the *Network Encoding (NE) Problem*, dates back at least to 1982 and has been most commonly studied in the context of the Hopfield model [19, 2, 17].

Consider a network on n neurons that is characterized by a real-valued $n \times n$ matrix W , where W_{ij} is the connection strength from the j th to the i th neuron. To each neuron we associate an activity variable, $x_i(t)$, that evolves in time according to a prescription for the network dynamics. An *encoded pattern* of the network,

$$\sigma \subset [n] \stackrel{\text{def}}{=} \{1, \dots, n\},$$

is a binary pattern that can be *activated*. This means there exists an external input to the network such that $x(t) = (x_1(t), \dots, x_n(t))$ converges to a steady state x^* (a stable fixed point) with support σ :

$$\sigma = \text{supp}(x^*) \stackrel{\text{def}}{=} \{i \in [n] \mid x_i^* > 0\}.$$

For a given choice of network dynamics, the matrix W determines the set of encoded patterns of the network; we call this set the *code* of the network, and denote it $\mathcal{C}(W) \subset 2^{[n]}$, where $2^{[n]}$ is the set of all binary patterns (i.e., all subsets of $[n]$).

NE Problem. Given a prescribed set of binary patterns, $\mathcal{P} \subset 2^{[n]}$, find a network W such that $\mathcal{P} \subseteq \mathcal{C}(W)$, while minimizing the number of unwanted *spurious states*, which are the elements of $\mathcal{C}(W) \setminus \mathcal{P}$.

We say that a network W is an *exact solution* to the NE problem for \mathcal{P} if there are no spurious states, i.e. if $\mathcal{C}(W) = \mathcal{P}$. Under what conditions are exact solutions possible? If we do not have an exact solution, what are the spurious states and how can we control them? Is there a biologically plausible *encoding rule* that can be used to construct W from \mathcal{P} ?

We take a new look at the NE problem using networks of threshold-linear neurons. To find solutions, we investigate a simple encoding rule that operates on an inhibitory network and selectively switches “on” excitatory synapses between neurons that co-appear in one or more patterns. A key feature of this rule is the use of *binary graded* synapses. That is, we assume the excitatory synaptic connections between pairs of neurons are not only *binary*, in the sense that each synapse has only two states (“on” or “off”), but also *graded*, because

C. Curto
University of Nebraska-Lincoln, Lincoln, NE
E-mail: ccurto2@math.unl.edu

A. Degeratu
Albert-Ludwig-Universität, Freiburg, Germany
E-mail: anda.degeratu@math.uni-freiburg.de

V. Itskov
University of Nebraska-Lincoln, Lincoln, NE
E-mail: vladimir.itskov@math.unl.edu

connection strengths may vary from one synapse to another. The strengths of “on” synapses are considered to be predetermined by the underlying architecture of the network, and are given by a *synaptic strength matrix* S . There is, in fact, experimental evidence for hippocampal synapses that appear binary in this sense [29], with individual synapses exhibiting potentiation in an all-or-nothing fashion, but having different “thresholds” for potentiation and heterogeneous synaptic strengths.

Although the NE problem has typically been studied assuming uncorrelated (near-orthogonal) neural activity patterns, we make no such assumptions on \mathcal{P} . In fact, a central motivation for our present work stems from the problem of encoding heavily overlapping patterns corresponding to neural codes in cortical and hippocampal areas. A simple but important example is the case of *place field codes* (PF codes) in the hippocampus, where single neuron activity is characterized by place fields [26, 27]. Because place fields overlap, the activity patterns comprising a PF code are highly overlapping.

Our main results, Theorems 2 and 3, precisely characterize the codes $\mathcal{C}(W)$ that are obtained using our encoding rule and, more generally, the sets \mathcal{P} of binary patterns that admit exact solutions to the NE problem via symmetric threshold-linear networks. When \mathcal{P} is *not* encoded exactly, we are able to describe the spurious states, and find that they correspond to cliques in the “co-firing” graph of \mathcal{P} . These results imply that when \mathcal{P} is a one-dimensional PF code, our encoding rule naturally yields exact solutions to the NE problem for \mathcal{P} . In the case of two-dimensional PF codes, we generically obtain near-exact solutions, as there are very few spurious states. Moreover, after applying our encoding rule to a random subsampling of patterns, the spurious states that arise are typically elements of the full PF code. We suggest that – in this context – spurious states can be advantageous, allowing PF codes to be efficiently encoded from a highly undersampled set of patterns.

Our results use ideas from classical distance and convex geometry, such as Cayley-Menger determinants [8] and Helly’s theorem [5], establishing a novel connection between these areas of mathematics and neural network theory.

Background

Threshold-linear networks. A *threshold-linear network* is a firing rate model for a recurrent network [13, 15, 16] where the neurons all have threshold nonlinearity, $\phi(y) = [y]_+ = \max\{y, 0\}$. The dynamics are given

by,

$$\frac{dx_i}{dt} = -\frac{1}{\tau_i}x_i + \phi\left(\sum_{j=1}^n W_{ij}x_j + e_i - \theta_i\right), \quad i = 1, \dots, n,$$

where n is the number of neurons, $x_i(t)$ is the firing rate of the i th neuron at time t , e_i is the external input to the i th neuron, and $\theta_i > 0$ is its threshold. W_{ij} denotes the effective strength of the recurrent connection from the j th to the i th neuron, and the timescale $\tau_i > 0$ gives the rate at which a neuron’s activity decays to zero in the absence of any inputs. Although sigmoids more closely match experimentally measured input-output curves for neurons, the above threshold nonlinearity is often a good approximation when neurons are far from saturation [13, 31]. Assuming that encoded patterns of a network are in fact realized by neurons that are firing far from saturation, it is reasonable to approximate them as stable fixed points of the threshold-linear dynamics.

We can express the dynamics more compactly as

$$\dot{x} = -Dx + [Wx + b]_+, \quad (1)$$

where $D \stackrel{\text{def}}{=} \text{diag}(1/\tau_1, \dots, 1/\tau_n)$ is the diagonal matrix of inverse time constants, $b = (b_1, \dots, b_n) \in \mathbb{R}^n$ with $b_i = e_i - \theta_i$, and $[\cdot]_+$ is applied elementwise. Note that, unlike in the Hopfield model, the “input” to the network comes in the form of a constant external drive, b , rather than an initial condition $x(0)$.

The matrix D will be considered fixed, with strictly positive diagonal. We will assume homogeneous timescales and use $D = I$ (the identity matrix) for the Encoding Rule, but all results apply equally well to heterogeneous timescales. We also assume that $-D + W$ has strictly negative diagonal, so that the activity of an individual neuron always decays to zero in the absence of external or recurrent inputs. Although we consider responses to the full range of inputs $b \in \mathbb{R}^n$, the possible steady states of (1) are sharply constrained by the connectivity matrix W . Assuming fixed D , we refer to a particular threshold-linear network simply as W .

Recall that the code $\mathcal{C}(W)$ is the set of all encoded patterns of W , and that encoded patterns are binary patterns that can be activated as steady states in response to external input. For threshold-linear networks, an encoded pattern is exactly the same as a *stable set* (a.k.a. “permitted set” [16]) of the network, which is a non-empty subset of neurons $\sigma \subset [n]$ with the property that, for at least one external input $b \in \mathbb{R}^n$, there exists an asymptotically stable fixed point x^* such that $\sigma = \text{supp}(x^*)$ [11]. It has been previously shown that stable sets of W correspond to stable principal submatrices of $-D + W$ [11, Theorem 1.2] (see also [16] for a

proof specific to the symmetric case). As usual, a *stable matrix* is a matrix whose eigenvalues all have strictly negative real part. For any $n \times n$ matrix A , the notation A_σ denotes the *principal submatrix* obtained by restricting to the index set σ ; if $\sigma = \{s_1, \dots, s_k\}$, then A_σ is the $k \times k$ matrix with $(A_\sigma)_{ij} = A_{s_i s_j}$. We denote the set of all stable principal submatrices of A as

$$\text{stab}(A) \stackrel{\text{def}}{=} \{\sigma \subset [n] \mid A_\sigma \text{ is a stable matrix}\}.$$

We can now state the relevant implications of the above.

Theorem 1 *Let W be a threshold-linear network on n neurons with dynamics given by equation (1), and let $\mathcal{C}(W)$ be the code of W . The following two statements hold:*

1. $\mathcal{C}(W) = \text{stab}(-D + W)$.
2. If W is symmetric, then there exists a symmetric $n \times n$ matrix A with zero diagonal such that

$$\mathcal{C}(W) = \text{stab}(-11^T + A),$$

where -11^T denotes the $n \times n$ matrix of all -1 s.

Statement 1 is a direct consequence of [11, Theorem 1.2]. Statement 2 is Lemma 6 in the Appendix.

Theorem 1 allows one to find all encoded patterns of a given network. Our primary interest, however, is in the inverse problem: *Given a set of patterns \mathcal{P} , can we find a network W that encodes precisely those patterns?* Theorem 1 implies that \mathcal{P} admits an exact solution to the NE problem if and only if there exists a W such that $\mathcal{P} = \text{stab}(-D + W)$. From this it is easy to infer that exact solutions do not always exist (see Corollary 3 in the Appendix). *If W is not an exact solution for \mathcal{P} , then what are the spurious states?* We tackle these questions by analyzing the following Encoding Rule. Although this rule yields a restricted set of networks W , we will see that the corresponding $\mathcal{C}(W)$ encompass all possible codes that can be generated by *symmetric* threshold-linear networks.

Encoding Rule. The encoding rule is a prescription for obtaining a network W from a set of binary patterns $\mathcal{P} \subset 2^{[n]}$.

Step 1: Fix an $n \times n$ synaptic strength matrix S and an $\varepsilon > 0$. We think of S and ε as *intrinsic* properties of the underlying network architecture, established prior to encoding. We use a symmetric encoding rule, and so require that $S_{ij} = S_{ji} \geq 0$ and $S_{ii} = 0$.

Step 2: The network W is initialized to be symmetric with effective connection strengths $W_{ij} = W_{ji} < -1$ for $i \neq j$, and $W_{ii} = 0$. (Beyond this requirement, the initial values of W do not affect our results.)

Step 3: Following presentation of each pattern $\sigma \in \mathcal{P}$, we turn “on” all excitatory synapses between neurons that co-appear in σ . This means we update the relevant entries of W as follows:

$$W_{ij} := -1 + \varepsilon S_{ij} \text{ if } i, j \in \sigma \text{ and } i \neq j.$$

In particular, the order of presentation does not matter, and once an excitatory connection has been turned “on,” the value of W_{ij} stays the same regardless of the remaining patterns.

Note that this rule is Hebbian and *local*; i.e., each synapse is updated only in response to the co-activation of the two adjacent neurons, and the updates can be implemented by presenting only one pattern at a time [19, 13].

To better understand what kinds of networks and codes result from applying the Encoding Rule, observe that any initial W in Step 2 can be written as $W_{ij} = -1 - \varepsilon R_{ij}$, where $R_{ij} = R_{ji} > 0$ for $i \neq j$ and $R_{ii} = -1/\varepsilon$, so that $W_{ii} = 0$. Assuming a threshold-linear network with homogeneous timescales, i.e. fixing $D = I$, the final network W obtained from \mathcal{P} after Step 3 satisfies,

$$(-D + W)_{ij} = \begin{cases} -1 + \varepsilon S_{ij}, & \text{if } (ij) \in G(\mathcal{P}) \\ -1, & \text{if } i = j \\ -1 - \varepsilon R_{ij} & \text{if } (ij) \notin G(\mathcal{P}), \end{cases} \quad (2)$$

where $G(\mathcal{P})$ is the graph on n vertices (neurons) having an edge for each pair of neurons that co-appear in one or more patterns of \mathcal{P} . We call this graph the *co-firing graph* of \mathcal{P} . In essence, the rule allows the network to “learn” $G(\mathcal{P})$, selecting which excitatory synapses are turned “on” and assigned to their predetermined weights.

Any matrix $-D + W$ obtained via this rule has the form $-11^T + \varepsilon A$, where A is a symmetric matrix with zero diagonal and off-diagonal entries $A_{ij} = S_{ij} \geq 0$ or $A_{ij} = -R_{ij} < 0$, depending on \mathcal{P} . It follows from part 1 of Theorem 1 that the code of this network is given by

$$\mathcal{C}(W) = \text{stab}(-11^T + \varepsilon A).$$

Furthermore, we know by part 2 of Theorem 1 that the code of *any* symmetric W is of this form. Hence, although the Encoding Rule cannot produce all symmetric networks W , it does yield all possible *codes*, $\mathcal{C}(W)$, corresponding to symmetric threshold-linear networks.

What does the symmetry of W tell us about $\mathcal{C}(W)$ and, more generally, the dynamics of the network? It is easy to see that if W is symmetric, the code $\mathcal{C}(W) = \text{stab}(-D + W)$ has the structure of a simplicial

complex.¹ Recall that an (abstract) *simplicial complex* $\Delta \subset 2^{[n]}$ is a set of subsets of $[n]$ such that the following two properties hold: (1) for each $i \in [n]$, $\{i\} \in \Delta$, and (2) if $\sigma \in \Delta$ and $\tau \subset \sigma$, then $\tau \in \Delta$. Property 1 always holds for $\text{stab}(-D + W)$, because $-D + W$ has strictly negative diagonal. To check property 2, note that if the matrix $-D + W$ is symmetric then Cauchy’s interlacing theorem applies (Theorem 4 in the Appendix). A consequence of this theorem is that any principal submatrix of a stable symmetric matrix is itself stable (Corollary 4 in the Appendix), and so $\text{stab}(-D + W)$ satisfies property 2. We are not currently aware of any example of a simplicial complex that is not realizable as the code of a symmetric threshold-linear network, although it is likely that such examples exist.

In addition to being symmetric, the Encoding Rule (for small enough ε) generates “lateral inhibition” networks where the matrix $-D + W$ has strictly negative entries; in particular, $D - W$ is copositive. It follows from [16, Theorem 1] that for all input vectors $b \in \mathbb{R}^n$ and for all initial conditions, the network dynamics (1) converge to a stable fixed point.

Main Results

Our main results, Theorems 2 and 3, characterize the codes $\mathcal{C}(W)$ obtained using the Encoding Rule, as well as all sets of binary patterns \mathcal{P} that admit exact solutions to the NE problem via symmetric threshold-linear networks. In particular, we find that all clique complexes and their k -skeleta admit exact solutions, a fact that plays an important role when we later investigate encoding of PF codes.

Recall that the code of any symmetric network on n neurons has the form $\mathcal{C}(W) = \text{stab}(-11^T + \varepsilon A)$, for $\varepsilon > 0$ and A a symmetric $n \times n$ matrix with zero diagonal.² Describing such a code requires understanding the stability of principal submatrices that are all of the form $-11^T + \varepsilon A_\sigma$, which motivates the question:

Given $\varepsilon > 0$ and any symmetric matrix A with zero diagonal, when is $-11^T + \varepsilon A$ a stable matrix?

The answer to this question emerges from a surprising connection to classical distance geometry, a field that grew around the problem of finding conditions for a finite set of distances to be realizable from a configura-

tion of points in Euclidean space [8]. In what follows, square distance matrices will play a central role.

Definition 1 An $n \times n$ matrix A is a (Euclidean) *square distance matrix* if there exists a configuration of points $p_1, \dots, p_n \in \mathbb{R}^{n-1}$ (not necessarily distinct) such that $A_{ij} = \|p_i - p_j\|^2$. A is a *nondegenerate* square distance matrix if the corresponding points are affinely independent; i.e., if the convex hull of p_1, \dots, p_n is a simplex with nonzero volume in \mathbb{R}^{n-1} .

A key object for determining whether or not A is a nondegenerate square distance matrix is the *Cayley-Menger determinant*, defined as

$$\text{cm}(A) \stackrel{\text{def}}{=} \det \begin{bmatrix} 0 & 1^T \\ 1 & A \end{bmatrix},$$

where $1 \in \mathbb{R}^n$ is the column vector of all ones. It is well-known that if A is a square distance matrix, $\text{cm}(A)$ is proportional to the square volume of the simplex obtained as the convex hull of the points $\{p_i\}$ (see Lemma 8, in the Appendix). In particular, $|\text{cm}(A)| > 0$ if A is a *nondegenerate* square distance matrix, while $\text{cm}(A) = 0$ for any other (degenerate) square distance matrix.

With these notions from distance geometry, we can now answer the above question.

Proposition 1 *Let $\varepsilon > 0$, and let A be a symmetric $n \times n$ matrix with zero diagonal. Then the matrix*

$$-11^T + \varepsilon A$$

is stable if and only if the following two conditions hold:

- (a) *A is a nondegenerate square distance matrix, and*
- (b) *$0 < \varepsilon < |\text{cm}(A)/\det(A)|$.*

Proposition 1 is a special case of Theorem 5, our core technical result, whose statement and proof are given in the Appendix.

The ratio $|\text{cm}(A)/\det(A)|$ has a simple geometric interpretation (see Remark 1 in the Appendix). Moreover, since $|\text{cm}(A)| > 0$ whenever A is a nondegenerate square distance matrix, there always exists an ε small enough to satisfy the second condition, provided the first condition holds. Combining Proposition 1 together with Cauchy’s interlacing theorem yields:

Lemma 1 *If A is an $n \times n$ nondegenerate square distance matrix, then*

$$0 < \left| \frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} \right| \leq \left| \frac{\text{cm}(A_\tau)}{\det(A_\tau)} \right| \quad \text{if } \tau \subseteq \sigma \subseteq [n].$$

¹ This was first observed in [16], using a version of Theorem 1 for symmetric W .

² In fact, any code of this form can be obtained by perturbing around any rank 1 matrix – not necessarily symmetric – having strictly negative diagonal (Proposition 2, in the Appendix).

Given any symmetric $n \times n$ matrix A with zero diagonal, and $\varepsilon > 0$, it is now natural to define two simplicial complexes in $2^{[n]}$:

$$\begin{aligned} \text{geom}_\varepsilon(A) &\stackrel{\text{def}}{=} \{\sigma \subseteq [n] \mid A_\sigma \text{ a nondeg. sq. dist. matrix,} \\ &\quad \text{and } 0 < \varepsilon < \left| \frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} \right| \}, \text{ and} \\ \text{geom}(A) &\stackrel{\text{def}}{=} \lim_{\varepsilon \rightarrow 0} \text{geom}_\varepsilon(A) \\ &= \{\sigma \subseteq [n] \mid A_\sigma \text{ a nondeg. sq. dist. matrix}\}. \end{aligned}$$

Note that if $\sigma = \{i\}$, we have $A_\sigma = [0]$. In this case, $\{i\} \in \text{geom}(A)$ and $\{i\} \in \text{geom}_\varepsilon(A)$ for all $\varepsilon > 0$, by our convention.

Lemma 1 implies that $\text{geom}_\varepsilon(A)$ and $\text{geom}(A)$ are simplicial complexes, and $\text{geom}_\varepsilon(A) = \text{geom}(A)$ if and only if $0 < \varepsilon < \delta(A)$, where

$$\delta(A) \stackrel{\text{def}}{=} \min \left\{ \left| \frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} \right| \right\}_{\sigma \in \text{geom}(A)}.$$

It also follows from Lemma 1 that if A is a nondegenerate square distance matrix, then $\delta(A) = |\text{cm}(A)/\det(A)|$.

Applying Proposition 1 to each of the principal submatrices of the perturbed matrix $-11^T + \varepsilon A$ we obtain:

Corollary 1 *If A is a symmetric matrix with zero diagonal, and $\varepsilon > 0$, then*

$$\text{stab}(-11^T + \varepsilon A) = \text{geom}_\varepsilon(A).$$

For $0 < \varepsilon < \delta(A)$, $\text{stab}(-11^T + \varepsilon A) = \text{geom}(A)$.

Next, recall that a *clique* in a graph G is a subset of vertices that is all-to-all connected. The *clique complex* of G , denoted $X(G)$, is the set of all cliques in G ; this is a simplicial complex for any G .

Corollary 2 *Let A be a symmetric $n \times n$ matrix with zero diagonal, and $\varepsilon > 0$. Let G be the graph on n vertices having $(ij) \in G$ if and only if $A_{ij} \geq 0$. For any $n \times n$ matrix S with $S_{ij} = S_{ji} \geq 0$ and $S_{ii} = 0$, if S “matches” A on G (i.e., if $S_{ij} = A_{ij}$ for all $(ij) \in G$), then*

$$\text{geom}_\varepsilon(A) = \text{geom}_\varepsilon(S) \cap X(G).$$

In particular, $\text{geom}(A) = \text{geom}(S) \cap X(G)$.

Recall that any $n \times n$ synaptic strength matrix S used in the Encoding Rule satisfies $S_{ij} = S_{ji} \geq 0$ and $S_{ii} = 0$ for all $i, j \in [n]$. We are now ready to state our main results.

Theorem 2 *Let S and $\varepsilon > 0$ be fixed, as in Step 1 of the Encoding Rule, and let W be the final threshold-linear network obtained from a prescribed set of patterns $\mathcal{P} \subset 2^{[n]}$ (equation (2)). Then,*

$$\mathcal{C}(W) = \text{geom}_\varepsilon(S) \cap X(G(\mathcal{P})).$$

If $\varepsilon < \delta(S)$, then

$$\mathcal{C}(W) = \text{geom}(S) \cap X(G(\mathcal{P})). \quad (3)$$

Proof Any network W obtained via the Encoding Rule (equation (2)) has the form $-D + W = -11^T + \varepsilon A$, where A is symmetric with zero diagonal and “matches” the (nonnegative) synaptic strength matrix S precisely on the entries A_{ij} such that $(ij) \in G(\mathcal{P})$. All other off-diagonal entries of A are negative. It follows that

$$\begin{aligned} \mathcal{C}(W) &= \text{stab}(-11^T + \varepsilon A) = \text{geom}_\varepsilon(A) \\ &= \text{geom}_\varepsilon(S) \cap X(G(\mathcal{P})), \end{aligned}$$

where the last two equalities are due to Corollaries 1 and 2, stemming from Proposition 1. \square

Next we identify a necessary and sufficient condition for \mathcal{P} to admit an exact solution to the NE problem via a symmetric network.

Theorem 3 *Let $\mathcal{P} \subset 2^{[n]}$. There exists a symmetric threshold-linear network W that is an exact solution to the NE problem for \mathcal{P} if and only if \mathcal{P} is a simplicial complex of the form*

$$\mathcal{P} = \text{geom}_\varepsilon(S) \cap X(G(\mathcal{P})), \quad (4)$$

for some $\varepsilon > 0$ and S an $n \times n$ matrix with $S_{ij} = S_{ji} \geq 0$ and $S_{ii} = 0$ for all $i, j \in [n]$. Moreover, W can be obtained using the Encoding Rule for \mathcal{P} .

Proof (\Leftarrow) This is an immediate consequence of Theorem 2. (\Rightarrow) Suppose there exists a symmetric network W with $\mathcal{C}(W) = \mathcal{P}$, and observe by Theorem 1 that $\mathcal{C}(W) = \text{stab}(-11^T + A)$, for some symmetric $n \times n$ matrix A with zero diagonal. By Corollaries 1 and 2,

$$\mathcal{P} = \mathcal{C}(W) = \text{geom}_\varepsilon(A) = \text{geom}_\varepsilon(S) \cap X(G),$$

where $\varepsilon = 1$, G is the graph associated to A (as in Corollary 2) and S is an $n \times n$ matrix with $S_{ij} = S_{ji} \geq 0$ and zero diagonal that “matches” A on G . It remains only to show that $\text{geom}_\varepsilon(S) \cap X(G) = \text{geom}_\varepsilon(S) \cap X(G(\mathcal{P}))$. Since $\mathcal{P} = \text{geom}_\varepsilon(A)$, any element $(ij) \in \mathcal{P}$ must have corresponding $A_{ij} > 0$, so $G(\mathcal{P}) \subseteq G$ and hence $X(G(\mathcal{P})) \subseteq X(G)$. On the other hand, $\mathcal{P} = \mathcal{P} \cap X(G(\mathcal{P}))$, so we conclude that $\mathcal{P} = \text{geom}_\varepsilon(S) \cap X(G(\mathcal{P}))$. \square

Remarks. As an immediate consequence of Theorem 2, we know that all clique complexes can be exactly encoded in threshold-linear networks.³ If \mathcal{P} is a clique complex on n vertices (neurons), then $\mathcal{P} = X(G(\mathcal{P}))$.

³ For recent work encoding cliques in Hopfield networks, see [18].

Fix S to be any $n \times n$ nondegenerate square distance matrix, and let $0 < \varepsilon < \delta(S) = |\text{cm}(S)/\det(S)|$. Then $\text{geom}_\varepsilon(S) = \text{geom}(S) = 2^{[n]}$, and hence by Theorem 2 the network W obtained from \mathcal{P} via the Encoding Rule is an exact solution, as its code is given by $\mathcal{C}(W) = X(G(\mathcal{P})) = \mathcal{P}$.

If \mathcal{P} is the k -skeleton⁴ of a clique complex on n vertices, with $k < n - 1$, then

$$\mathcal{P} = X_k(G(\mathcal{P})) \stackrel{\text{def}}{=} \{\sigma \in X(G(\mathcal{P})) \mid |\sigma| \leq k + 1\}.$$

Any such \mathcal{P} can also be exactly encoded. Fix S to be a (degenerate) $n \times n$ square distance matrix for a configuration of n points that are in general position in \mathbb{R}^k , and let $0 < \varepsilon < \delta(S)$. Then $\text{geom}_\varepsilon(S) = \text{geom}(S) = \{\sigma \subset [n] \mid |\sigma| \leq k + 1\}$ is the k -skeleton of $2^{[n]}$. Since $\text{geom}(S) \cap X(G(\mathcal{P})) = X_k(G(\mathcal{P}))$, Theorem 2 implies that the network W obtained from \mathcal{P} via the Encoding Rule is an exact solution to the NE problem for \mathcal{P} .

It is worth noting here that solutions obtained using a degenerate square distance matrix S are not as fine-tuned as they might first appear. This is because the ratio $|\text{cm}(S_\sigma)/\det(S_\sigma)|$ approaches zero as subsets of points $\{p_i\}_{i \in \sigma}$ become *approximately* degenerate, allowing elements to be eliminated from $\text{geom}_\varepsilon(S)$ because of violations to condition (b) in Proposition 1, even if condition (a) is not quite violated (see Remark 2 in the Appendix).

Spurious states, Helly's theorem, and Place Field codes

Recall that our Encoding Rule assumes the synaptic strength matrix S is an intrinsic property of the underlying network. Theorem 2 implies that certain “universal” choices of S enable any $\mathcal{P} \subset 2^{[n]}$ to be encoded, yielding $\mathcal{C}(W) = X(G(\mathcal{P})) \supseteq \mathcal{P}$. The price to pay, however, is the emergence of spurious states.

Spurious states. Recall that spurious states are elements of $\mathcal{C}(W)$ that are *not* in the prescribed list \mathcal{P} . We can divide them into two types: the first type consists of encoded patterns $\sigma \in \mathcal{C}(W) \setminus \mathcal{P}$ that are subsets of patterns in \mathcal{P} , while the second type consists of all other elements of $\mathcal{C}(W) \setminus \mathcal{P}$. The first type of spurious states are guaranteed to be present for any symmetric encoding rule, unless \mathcal{P} is a simplicial complex. This is because $\text{stab}(-D + W)$ is a simplicial complex for symmetric W . It is not clear, however, that these states should be considered truly “spurious,” since they correspond

to partial patterns whose retrieval does not necessarily constitute an “error” on the part of the network. For this reason, we restrict attention to the second type, as was previously done in [33]. The second type of spurious states contains all $\sigma \in \mathcal{C}(W)$ such that σ is *not* a subset of any $\tau \in \mathcal{P}$. Because each such σ resulting from our Encoding Rule is an element of $X(G(\mathcal{P}))$, we will refer to these states from now on as *spurious cliques*.

Perhaps surprisingly, some common neural codes have the property that the full set of patterns to be encoded naturally contains most of the cliques in the code's co-firing graph, so that $\mathcal{P} \approx X(G(\mathcal{P}))$. Such codes have very few spurious cliques. This is precisely the case for PF codes.

PF codes. Let $\{U_1, \dots, U_n\}$ be a collection of convex open sets in \mathbb{R}^d , where each U_i is the *place field* corresponding to the i th neuron. To such a set of place fields we associate a d -dimensional PF code, \mathcal{P} , defined as follows: for each $\sigma \in 2^{[n]}$, $\sigma \in \mathcal{P}$ if and only if the intersection $\bigcap_{i \in \sigma} U_i$ is nonempty. PF codes are combinatorial neural codes; note that this definition yields a simplicial complex, called the *nerve* of the cover [9].

PF codes are experimentally observed in recordings of neural activity in rodent hippocampus [23]. The elements of \mathcal{P} correspond to subsets of neurons that may be co-activated as the animal's trajectory passes through a corresponding set of overlapping place fields. Typically $d = 1$ or $d = 2$, corresponding to the standard “linear track” and “open field” environments [24]; it has also been hypothesized that some animals possess $d = 3$ place fields [32].

Since \mathcal{P} is a simplicial complex, encoding a PF code using the Encoding Rule produces no spurious states of the first type. What about spurious cliques? Remarkably, there are very few of them, since most cliques in $X(G(\mathcal{P}))$ are already contained in \mathcal{P} . This follows from the classical Helly's theorem [5].

Helly's theorem. Suppose that U_1, \dots, U_k is a finite collection of convex subsets of \mathbb{R}^d , for $d < k$. If the intersection of any $d + 1$ of these sets is nonempty, then the full intersection $\bigcap_{i=1}^k U_i$ is also nonempty. To see the implications of Helly's theorem for PF codes, we first define the notion of *Helly completion*:

Definition 2 Let Δ be a simplicial complex on n vertices, and let $\Delta_d = \{\sigma \in \Delta \mid |\sigma| \leq d + 1\}$ denote its d -skeleton. The *Helly completion* is the largest simplicial complex, $\bar{\Delta}_d$, on n vertices that has Δ_d as its d -skeleton.

For example, the $d = 1$ Helly completion of a graph G is the clique complex $X(G)$. Helly's theorem can now be reformulated as:

⁴ The k -skeleton of a simplicial complex is obtained by restricting to faces of dimension $\leq k$, which corresponds to elements $\sigma \subset [n]$ of size $|\sigma| \leq k + 1$.

Lemma 2 Let \mathcal{P} be a d -dimensional PF code, corresponding to a set of place fields $\{U_1, \dots, U_n\}$ where each U_i is a convex open set in \mathbb{R}^d . Then \mathcal{P} is the Helly completion of its own d -skeleton: $\mathcal{P} = \bar{\mathcal{P}}_d$.

In particular, any one-dimensional PF code is always a clique complex, and thus has an exact solution to the NE problem that can be obtained using the Encoding Rule. A two-dimensional PF code \mathcal{P} is the Helly completion of its own 2-skeleton, which can be obtained from knowledge of all pairwise and triple intersections of place fields. The only possible spurious cliques are therefore spurious triples and the larger cliques of $G(\mathcal{P})$ that contain them. These spurious triples emerge when three place fields U_i, U_j and U_k have the property that each pair intersect, but $U_i \cap U_j \cap U_k = \emptyset$.

Encoding sparse PF codes in threshold-linear networks

Helly’s theorem sharply limits the number of spurious cliques that result from encoding two-dimensional PF codes. For “sparse” PF codes, we find that spurious cliques can be further restricted by an appropriate choice of S . We also find that PF codes can be encoded from a very small, random sample of patterns. The near-exact encoding of PF codes from highly undersampled data makes them quite natural codes in the context of threshold-linear networks.

Controlling spurious cliques in sparse codes. Experimentally observed neural activity in cortical and hippocampal areas suggests that neural codes are *sparse* [21, 4], meaning that few neurons are co-active in response to stimuli. If the set of patterns $\mathcal{P} \subset 2^{[n]}$ to be encoded is a k -sparse code, i.e. if $|\sigma| \leq k < n$ for all $\sigma \in \mathcal{P}$, then any clique of size $k + 1$ or greater in $G(\mathcal{P})$ is potentially spurious. We can eliminate these spurious states, however, by choosing S in the Encoding Rule to be a degenerate square distance matrix for a configuration of points $p_1, \dots, p_n \in \mathbb{R}^{k-1}$ and $0 < \varepsilon < \delta(S)$. This guarantees that $\text{geom}_\varepsilon(S)$ does not include any element of size greater than k , and hence $\mathcal{C}(W) \subseteq X_{k-1}(G(\mathcal{P}))$. Note that such a choice of S is “universal,” as it works for any code \mathcal{P} of sparsity k .

Near-exact encoding of sparse PF codes. Consider a two-dimensional PF code \mathcal{P} that is k -sparse, so that no more than k neurons can co-fire in a single pattern – even if there are higher-order overlaps of place fields. Experimental evidence suggests that the fraction of active neurons is typically on the order of 5 – 10% [3], so we make the conservative choice of $k = .1n$ (our

results improve with smaller k). In what follows, S and ε are chosen as above to control spurious cliques of size greater than k , and we assume the worst-case-scenario of $\mathcal{C}(W) = X_{k-1}(G(\mathcal{P}))$, providing an upper bound on the number of spurious cliques resulting from our Encoding Rule. What fraction of the encoded patterns are spurious? This can be quantified by the following *error probability*:

$$P_{\text{error}} \stackrel{\text{def}}{=} \frac{|\mathcal{C}(W) \setminus \mathcal{P}|}{|\mathcal{C}(W)|} = \frac{|X_{k-1}(G(\mathcal{P}))| - |\mathcal{P}|}{|X_{k-1}(G(\mathcal{P}))|}.$$

For exact encoding, $P_{\text{error}} = 0$, while large numbers of spurious states will push P_{error} close to 1.

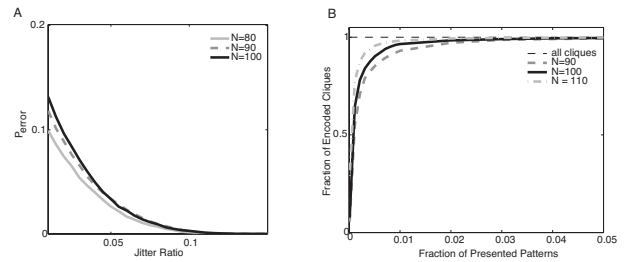


Fig. 1 PF encoding is near-exact, and can be achieved by presenting a small fraction of patterns. (A) P_{error} was computed for randomly generated k -sparse PF codes having $n = 80, 90$ and 100 neurons and $k = .1n$. For each jitter ratio, the average value of P_{error} over 100 codes is shown. (B) For $n = 90, 100$ and 110 neurons, k -sparse PF codes with jitter ratio 0.1 were randomly generated and then randomly subsampled to contain a small fraction ($\leq 5\%$) of the total number of patterns. After applying the Encoding Rule to the subsampled code, the number of encoded cliques was computed. In each case, the fraction of encoded cliques for the subsampled code (as compared to the full PF code) was averaged over 10 codes. Cliques were counted using Cliquer [25], together with custom-made Matlab software.

To investigate how “exactly” two-dimensional PF codes are encoded, we generated random k -sparse PF codes with circular place fields, $n = 80$ - 100 neurons, and $k = .1n$ (see the Appendix). Because experimentally observed place fields do not have precise boundaries, we also generated “jittered” codes, where spurious triples were eliminated from the 2-skeleton of the code if they did not survive after enlarging the place field radii from r_0 to r_1 by a *jitter ratio*, $(r_1 - r_0)/r_0$. This has the effect of eliminating spurious cliques that are unlikely to be observed in neural activity, as they correspond to very small regions in the underlying environment. For each code and each jitter ratio (up to ~ 0.1), we computed P_{error} using the formula above. Even without jitter, the error probability was small, and P_{error} decreased quickly to values near zero for 10% jitter (Fig. 1A).

Encoding full PF codes from highly undersampled sets of patterns. To investigate what fraction of patterns is needed to encode a two-dimensional PF code using the Encoding Rule, we generated randomly subsampled codes from k -sparse PF codes. We then computed the number of patterns that would be encoded by a network if a subsampled code was presented. Perhaps surprisingly, network codes obtained from highly subsampled PF codes (having only 1-5% of the patterns) are nearly identical to those obtained from full PF codes (Fig. 1B). This is because large numbers of “spurious” states emerge when encoding subsampled codes, but most correspond to patterns in the full code. The spurious states of subsampled PF codes can therefore be *advantageous*, allowing networks to quickly encode full PF codes from only a small fraction of the patterns.

Exact solutions to the NE problem

We have seen that clique complexes and k -skeleta of clique complexes can all be encoded exactly, and two-dimensional PF codes can be encoded nearly exactly, *without* tuning the synaptic strength matrix S as a function of the patterns to be encoded. If, instead, we are allowed to tune S as a function of \mathcal{P} , it is clear from Theorem 3 that we can obtain exact solutions to the NE problem for a wider class of simplicial complexes. In particular, if $\mathcal{P} = \text{geom}(S)$ for some $n \times n$ matrix S satisfying $S_{ij} = S_{ji} \geq 0$ and $S_{ii} = 0$, then $\mathcal{C}(W) = \mathcal{P}$ after applying the Encoding Rule with this S and $0 < \varepsilon < \delta(S)$. It follows that any \mathcal{P} of the form $\text{geom}(S)$ admits an exact solution to the NE problem.

In the special case where S is a square distance matrix, $\text{geom}(S)$ is a *representable matroid complex* – i.e., it is the independent set complex of a real-representable matroid [28]. Moreover, it is easy to see that all representable matroid complexes are of this form, and can thus be encoded exactly. In addition, Theorem 3 implies that we can exactly encode any $\mathcal{P} \subset 2^{[n]}$ of the form $\mathcal{P} = \Delta \cap X(G)$, where Δ is a representable matroid complex and $X(G)$ is the clique complex of a graph. The following example is of this type.

Example. Suppose \mathcal{P} is the two-dimensional simplicial complex on $n = 6$ neurons depicted in Figure 2A. \mathcal{P} is clearly not a clique complex or the k -skeleton of a clique complex, nor is \mathcal{P} a representable matroid complex, as it violates the independent set exchange property [28]. Nevertheless, there are exact solutions to the NE problem for \mathcal{P} . One exact solution can be obtained by choosing S to be the square distance matrix corresponding to the configuration of points in Figure 2B. Another exact solution arises by constructing an S that

is *not* a square distance matrix, but has select principal submatrices that are (see the Appendix).

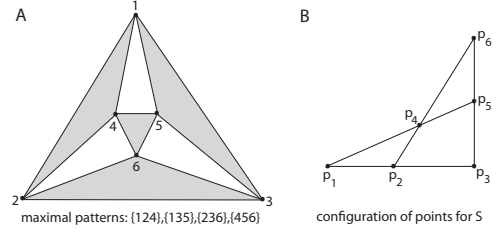


Fig. 2 An example on $n = 6$ neurons. (A) A simplicial complex \mathcal{P} consisting of four two-dimensional facets (shaded triangles). The graph $G(\mathcal{P})$ contains the 12 depicted edges. (B) A configuration of points $p_1, \dots, p_6 \in \mathbb{R}^2$ that can be used to exactly encode \mathcal{P} . Lines indicate triples of points that are collinear. From this configuration we construct a 6×6 synaptic strength matrix S , with $S_{ij} = \|p_i - p_j\|^2$, and choose $0 < \varepsilon < \delta(S)$. The geometry of the configuration implies that $\text{geom}(S)$ does not contain any patterns of size greater than 3, nor does it contain the triples $\{123\}$, $\{145\}$, $\{246\}$, or $\{356\}$. It is straightforward to check that $\mathcal{P} = \text{geom}(S) \cap X(G(\mathcal{P}))$.

Open questions. We conclude this section with some mathematical questions. Can a combinatorial description be found for all simplicial complexes that are of the form $\text{geom}_\varepsilon(S)$ or $\text{geom}(S)$, where S and ε satisfy the conditions in Theorem 3? For such complexes, can the appropriate S and ε be obtained constructively? Does every simplicial complex \mathcal{P} admit an exact solution to the NE problem via a *symmetric* network W ? I.e., is every simplicial complex of the form $\text{geom}_\varepsilon(S) \cap X(G(\mathcal{P}))$, as in equation (4)? If not, what are the obstructions? More generally, does every simplicial complex admit an exact solution (not necessarily symmetric) to the NE problem?

Discussion

Understanding the relationship between the connectivity matrix and the activity patterns of a neural network is one of the central challenges in theoretical neuroscience. We have found that in the context of threshold-linear networks, one can obtain an unexpectedly precise understanding of the binary activity patterns encoded by network steady states. In particular, we have shown that these networks naturally encode neural codes arising from low-dimensional receptive fields (such as place fields) while introducing very few spurious states. Remarkably, these codes can be “learned” by the network from a highly undersampled set of patterns.

Neural codes representing (continuous) parametric stimuli, such as place field codes, have typically been modeled as arising from continuous attractor networks

whose synaptic matrices have symmetric “Mexican hat”-type connectivity [6, 23]. This is in large part due to the fact that there is a well-developed mathematical handle on these networks [1, 10, 22]. Our work shows that one can have fine mathematical control over a much wider class of networks, encompassing all symmetric connectivity matrices. It may thus provide a novel foundation for understanding and “engineering” neural networks with prescribed steady state properties.

Acknowledgments The authors would like to thank Christopher Hillar, Caroline Klivans and Bernd Sturmfels for valuable discussions, and Zachary Roth for assistance with the Cliquer software. CC was supported by NSF DMS 0920845 and an Alfred P. Sloan Research Fellowship. AD was supported by the Max Planck Society and the DFG via SFB/Transregio 71 “Geometric Partial Differential Equations.” VI was supported by NSF DMS 0967377 and NSF DMS 1122519.

Appendix: Proofs and Supporting Text

Not all codes are realizable by threshold-linear networks

The following result applies to any square matrix A , not necessarily symmetric.

Lemma 3 *Let A be an $n \times n$ matrix with strictly negative diagonal and $n \geq 2$. If A is stable, then there exists a 2×2 principal submatrix of A that is also stable.*

Proof We use the formula for the characteristic polynomial in terms of sums of principal minors to obtain:

$$p_A(X) = (-1)^n X^n + (-1)^{n-1} m_1(A) X^{n-1} + (-1)^{n-2} m_2(A) X^{n-2} + \dots + m_n(A),$$

where $m_k(A)$ is the sum of the $k \times k$ principal minors of A . Writing the characteristic polynomial in terms of symmetric polynomials in the eigenvalues $\alpha_1, \alpha_2, \dots, \alpha_n$, and assuming A is stable, we have $m_2(A) = \sum_{i < j} \alpha_i \alpha_j > 0$. This implies that at least one 2×2 principal minor is positive. Since the corresponding 2×2 principal submatrix has negative trace, it must be stable. \square

Combining Lemma 3 with Theorem 1 we obtain:

Corollary 3 *Let $\mathcal{P} \subset 2^{[n]}$. If there exists a pattern $\sigma \in \mathcal{P}$ such that no order 2 subset of σ belongs to \mathcal{P} , then \mathcal{P} is not realizable as $\mathcal{C}(W)$ for any threshold-linear network W .*

Stable symmetric matrices

Here we summarize some well-known facts about the stability of symmetric matrices that we use in various proofs. The first is Cauchy’s interlacing theorem, which relates eigenvalues of a symmetric matrix to those of its principal submatrices.

Theorem 4 (Cauchy’s interlacing theorem [20])

Let A be a symmetric $n \times n$ matrix, and let B be an $m \times m$ principal submatrix of A . If the eigenvalues of A are $\alpha_1 \leq \dots \leq \alpha_n$ and those of B are $\beta_1 \leq \dots \leq \beta_m$, then $\alpha_j \leq \beta_j \leq \alpha_{n-m+j}$ for all j .

An immediate consequence of this theorem is:

Corollary 4 *Any principal submatrix of a stable symmetric matrix is stable. Any symmetric matrix containing an unstable principal submatrix is unstable.*

Another well-known consequence of Cauchy’s interlacing theorem is the following Lemma. Here $A_{[k]}$ refers to the principal submatrix obtained by taking the upper left $k \times k$ entries of A .

Lemma 4 *Let A be a real symmetric $n \times n$ matrix. Then the following are equivalent:*

1. A is a stable matrix.
2. $(-1)^k \det(A_{[k]}) > 0$ for all $1 \leq k \leq n$.
3. $(-1)^{|\sigma|} \det(A_\sigma) > 0$ for every $\sigma \subseteq [n]$.

Codes of symmetric networks

Recall from part 1 of Theorem 1 that all codes $\mathcal{C}(W)$, where W is a threshold-linear network with dynamics given by equation (1), have the form

$$\mathcal{C}(W) = \text{stab}(-D + W).$$

Here we show that when W is *symmetric* (like the networks obtained using the Encoding Rule (2)), $\mathcal{C}(W)$ can always be expressed as $\text{stab}(-11^T + A)$ or $\text{stab}(-xy^T + B)$, where $-xy^T$ is any rank 1 matrix having strictly negative diagonal, and A, B are square matrices with zero diagonal. In particular, Lemma 6 gives part 2 of Theorem 1.

In what follows, we use the notation

$$\mathbb{R}_\times^n \stackrel{\text{def}}{=} \{v \in \mathbb{R}^n \mid v_i \neq 0 \text{ for all } i \in [n]\},$$

for the set of vectors with all nonzero entries. Given a vector $v \in \mathbb{R}^n$ and an $n \times n$ matrix A ,

$$A^v \stackrel{\text{def}}{=} \text{diag}(v) A \text{diag}(v)$$

denotes the matrix with entries $A_{ij}^v = v_i v_j A_{ij}$. Note that for principal submatrices, $(A^v)_\sigma = (A_\sigma)^{v_\sigma}$, so we simply denote this matrix A_σ^v . This notation will also be used later, in Theorem 5.

Lemma 5 *Let M be a symmetric $n \times n$ matrix, and $v \in \mathbb{R}_\times^n$. Then,*

$$\text{stab}(M^v) = \text{stab}(M).$$

Proof By Lemma 4, $\tau \in \text{stab}(M)$ if and only if $(-1)^{|\sigma|} \det(M_\sigma) > 0$ for every $\sigma \subseteq \tau$. Observe that, since $M^v = \text{diag}(v)M \text{diag}(v)$, we have $\text{sgn}(\det(M_\sigma^v)) = \text{sgn}(\det(M_\sigma))$ for all $\sigma \subseteq [n]$. It follows that $\tau \in \text{stab}(M^v)$ if and only if $\tau \in \text{stab}(M)$. \square

Lemma 6 *For any symmetric threshold-linear network W on n neurons, there exists a symmetric $n \times n$ matrix A with zero diagonal such that*

$$\mathcal{C}(W) = \text{stab}(-11^T + A).$$

Proof Let $x \in \mathbb{R}_\times^n$ be the vector such that $\text{diag}(-xx^T) = \text{diag}(-D + W)$, and write

$$-D + W = -xx^T + (-D + W + xx^T),$$

where the term in parentheses is symmetric and has zero diagonal. This can be rewritten as

$$-D + W = \text{diag}(x)(-11^T + A) \text{diag}(x) = (-11^T + A)^x,$$

where

$$A = \text{diag}(x)^{-1}(-D + W + xx^T) \text{diag}(x)^{-1}$$

is a symmetric $n \times n$ matrix with zero diagonal. It follows from Lemma 5 that $\mathcal{C}(W) = \text{stab}(-D + W) = \text{stab}(-11^T + A)$. \square

Lemma 6 implies that all codes $\mathcal{C}(W)$ for symmetric networks W have the form $\mathcal{C}(W) = \text{stab}(-11^T + A)$, where A is a symmetric matrix having zero diagonal. The following Proposition implies that all such codes can also be obtained by perturbing around *any* rank 1 matrix with negative diagonal, not necessarily symmetric. Note that if $x, y \in \mathbb{R}_\times^n$, the rank 1 matrix $-xy^T$ has strictly negative diagonal if and only if $x_i y_i > 0$ for all $i \in [n]$.

Proposition 2 *Fix $x, y \in \mathbb{R}_\times^n$ with $x_i y_i > 0$ for all $i \in [n]$. For any symmetric threshold-linear network W on n neurons, there exists an $n \times n$ matrix B with zero diagonal such that*

$$\mathcal{C}(W) = \text{stab}(-xy^T + B).$$

The proof of this Proposition constructs the matrix B explicitly, and relies on the following Lemma.

Lemma 7 *Let M be any $n \times n$ matrix, and T an $n \times n$ invertible diagonal matrix. Then*

$$\text{stab}(TMT^{-1}) = \text{stab}(M).$$

Proof We have $(TMT^{-1})_\sigma = T_\sigma M_\sigma T_\sigma^{-1}$. Since conjugation preserves the eigenvalue spectrum, the statement follows. \square

Proof (Proof of Proposition 2) Let W be a symmetric threshold-linear network on n neurons. By Lemma 6, there exists a symmetric $n \times n$ matrix A with zero diagonal such that $\mathcal{C}(W) = \text{stab}(-11^T + A)$. It thus remains only to construct an $n \times n$ matrix B with zero diagonal such that

$$\text{stab}(-xy^T + B) = \text{stab}(-11^T + A).$$

We prove that this can always be done in two steps: first, we prove that it can be done in the special case $x = y$, and then we show that B can be constructed in general.

Step 1: Fix $x = y \in \mathbb{R}_\times^n$, and observe that $-xx^T + A^x = (-11^T + A)^x$, so by Lemma 5 we have $\text{stab}(-xx^T + A^x) = \text{stab}(-11^T + A)$. Letting $B = A^x$ we obtain the desired statement.

Step 2: Fix $x, y \in \mathbb{R}_\times^n$ so that $x_i y_i > 0$ for all $i \in [n]$, and let T be the diagonal matrix with entries $T_{ii} = \sqrt{y_i/x_i}$. Then

$$(T(-xy^T)T^{-1})_{ij} = \sqrt{\frac{y_i}{x_i}}(-x_i y_j) \sqrt{\frac{x_j}{y_j}} = -\sqrt{x_i y_i} \sqrt{x_j y_j},$$

so $T(-xy^T)T^{-1} = -zz^T$ for $z \in \mathbb{R}_\times^n$ having entries $z_i = \sqrt{x_i y_i}$. It follows from Step 1 that $\text{stab}(-11^T + A) = \text{stab}(-zz^T + A^z) = \text{stab}(T(-xy^T)T^{-1} + A^z)$. Let

$$B = T^{-1}A^z T.$$

Then, using Lemma 7, $\text{stab}(-xy^T + B) = \text{stab}(T(-xy^T + B)T^{-1}) = \text{stab}(-11^T + A)$. Since A has zero diagonal, so do A^z and B . Note that B can be obtained explicitly, using the expression for A in the proof of Lemma 6. \square

Statement of Theorem 5 and Proof of Proposition 1

Theorem 5 is our core technical result. It is closely related to some relatively recent results in convex geometry, involving correlation matrices and the geometry of the “elliptope” [14]. Our proof, however, relies only on classical distance geometry and well-known facts about stable symmetric matrices. Following the statement we prove Proposition 1 from the Main Text, which is essentially a special case.

Note that for $v \in \mathbb{R}_\times^n$, $-vv^T$ is a symmetric rank 1 matrix with strictly negative diagonal. We will also need the following definition.

Definition 3 A *Hebbian* matrix A is an $n \times n$ matrix satisfying $A_{ij} = A_{ji} \geq 0$ and $A_{ii} = 0$ for all $i, j \in [n]$.

The name reflects the fact that these are precisely the types of matrices that arise when synaptic weights are modified by a Hebbian learning rule.

Theorem 5 Fix $v \in \mathbb{R}_\times^n$, and consider the perturbed matrix,

$$M = -vv^T + \varepsilon A^v,$$

where A is a Hebbian matrix and $\varepsilon > 0$. Then the following are equivalent:

1. A is a nondegenerate square distance matrix.
2. There exists an $\varepsilon > 0$ such that M is stable.
3. There exists a $\delta > 0$ such that M is stable for all $0 < \varepsilon < \delta$.
4. $0 < -\frac{\text{cm}(A)}{\det A} < \infty$; and,

$$M \text{ is stable if and only if } 0 < \varepsilon < -\frac{\text{cm}(A)}{\det A}.$$

Proof (Proof of Proposition 1) Setting $v = 1 \in \mathbb{R}_\times^n$ (the column vector of all ones) in Theorem 5 yields a slightly weaker version of Proposition 1 from the Main Text, with the hypothesis that A is *Hebbian*, rather than merely symmetric with zero diagonal.

To see why Proposition 1 holds more generally, suppose A is symmetric with zero diagonal but *not* Hebbian. Then there exists an off-diagonal pair of negative entries, $A_{ij} = A_{ji} < 0$, and the 2×2 principal submatrix

$$(-11^T + \varepsilon A)_{\{ij\}} = \begin{pmatrix} -1 & -1 + \varepsilon A_{ij} \\ -1 + \varepsilon A_{ij} & -1 \end{pmatrix}$$

is unstable as it has negative trace and negative determinant. It follows from Cauchy's interlacing theorem (Corollary 4) that $-11^T + \varepsilon A$ is unstable for any $\varepsilon > 0$. Correspondingly, condition (a) in Proposition 1 is violated, as the existence of negative entries guarantees that A cannot be a nondegenerate square distance matrix. \square

Ingredients for the Proof of Theorem 5

Here we present some ingredients necessary for the proof of Theorem 5. First, we review some classical results about square distance matrices. Next, we present a “determinant lemma” that is critical for our proof.

Square distance matrices. Recall from the Main Text the definitions of square distance matrix, nondegenerate square distance matrix, and Cayley-Menger determinant. Our convention is that the 1×1 zero matrix $[0]$ is a nondegenerate square distance matrix, as $|\text{cm}([0])| = 1 > 0$. As an example, a 3×3 symmetric matrix A with zero diagonal is a nondegenerate square distance matrix if and only if the off-diagonal entries A_{ij}

are all positive, and their square roots ($\sqrt{A_{12}}, \sqrt{A_{13}}$, and $\sqrt{A_{23}}$) satisfy all three triangle inequalities.

There are two classical characterizations of square distance matrices. The first, due to Menger [8], relies on Cayley-Menger determinants. The second, due to Schoenberg [30], uses eigenvalues of principal submatrices. Both are needed for our proof of Theorem 5.

The relationship between Cayley-Menger determinants and simplex volumes is well-known:

Lemma 8 Let p_1, \dots, p_k be k points in a Euclidean space. Assume that $A_{ij} = \|p_i - p_j\|^2$ is the matrix of square distances between these points. Then the $(k-1)$ -dim volume V of the convex hull of the points $\{p_i\}_{i=1}^k$ can be computed as

$$V^2 = \frac{(-1)^k}{2^{(k-1)} ((k-1)!)^2} \text{cm}(A). \quad (5)$$

In particular, if A is a degenerate square distance matrix then $\text{cm}(A) = 0$.

This leads to Menger's characterization of square distance matrices. Recall that A_σ is the principal submatrix obtained by restricting A to the index set σ .

Lemma 9 Let A be an $n \times n$ matrix satisfying $A_{ij} = A_{ji} \geq 0$ and $A_{ii} = 0$ for all $i, j \in [n]$ (i.e., A is a Hebbian matrix). Then,

1. A is a square distance matrix if and only if $(-1)^{|\sigma|} \text{cm}(A_\sigma) \geq 0$ for every A_σ .
2. A is a nondegenerate square distance matrix if and only if $(-1)^{|\sigma|} \text{cm}(A_\sigma) > 0$ for every A_σ .

Proof (1) is equivalent to the Corollary of Theorem 42.2 in [8]. (2) is equivalent to Theorem 41.1 in [8]. \square

Schoenberg's characterization implies that if a matrix is a square distance matrix, then the determinant of any principal submatrix has opposite sign to that of its Cayley-Menger determinant.

Proposition 3 Let A be an $n \times n$ square distance matrix that is not the zero matrix. Then:

1. A has one strictly positive eigenvalue and $n-1$ eigenvalues that are less than or equal to zero. In particular, $(-1)^{|\sigma|} \det(A_\sigma) \leq 0$ for every principal submatrix A_σ .
2. If A is a nondegenerate square distance matrix, A has no zero eigenvalues and $(-1)^{|\sigma|} \det(A_\sigma) < 0$ for every principal submatrix A_σ with $|\sigma| > 1$.

Proof This Proposition is contained in [14, Theorem 6.2.16]. It can also be proven directly from Theorem 1 of Schoenberg's 1935 paper [30]. \square

Corollary 5 *If A is an $n \times n$ nondegenerate square distance matrix with $n > 1$, then*

$$-\frac{\text{cm}(A)}{\det A} > 0.$$

The determinant lemma. A cornerstone of the proof of Theorem 5 is the following lemma, which allows us to connect perturbations of symmetric rank 1 matrices to Cayley-Menger determinants. The statement is a bit more general, however, as $-uv^T$ can be any square matrix of rank 1.

Lemma 10 *Let $u, v \in \mathbb{R}^n$. Then for any real-valued $n \times n$ matrix A and any $t \in \mathbb{R}$,*

$$\begin{aligned} & \det(-uv^T + t \text{diag}(u)A \text{diag}(v)) \\ &= \det(\text{diag}(u) \text{diag}(v)) (t^n \det A + t^{n-1} \text{cm}(A)). \end{aligned}$$

In particular, if $u = v \in \mathbb{R}_\times^n$ and $t > 0$, then

$$\text{sgn}(\det(-vv^T + tA^v)) = \text{sgn}(t \det A + \text{cm}(A)),$$

where $\text{sgn} : \mathbb{R} \rightarrow \{\pm 1, 0\}$ detects the sign of the argument.

Corollary 6 $\det(-11^T + tA) = t^n \det A + t^{n-1} \text{cm}(A)$.

To prove Lemma 10, we use the following well-known formula for computing the determinant of a 2×2 block matrix:

$$\det \begin{bmatrix} A & B \\ C & D \end{bmatrix} = \det(A) \det(D - CA^{-1}B).$$

This applies so long as A is invertible. The formula follows from observing that

$$\begin{bmatrix} I & 0 \\ -CA^{-1} & I \end{bmatrix} \begin{bmatrix} A & B \\ C & D \end{bmatrix} = \begin{bmatrix} A & B \\ 0 & -CA^{-1}B + D \end{bmatrix}.$$

Proof (Proof of Lemma 10) Note that for any $n \times n$ matrix A , $t \in \mathbb{R}$, and $u, v \in \mathbb{R}^n$, we have

$$\begin{aligned} & \det(-uv^T + t \text{diag}(u)A \text{diag}(v)) = \\ & \det(\text{diag}(u) \text{diag}(v)) \det(-11^T + tA), \end{aligned}$$

where 11^T is the rank 1 matrix of all 1's. It thus suffices to show that

$$\det(-11^T + tA) = t^n \det A + t^{n-1} \text{cm}(A),$$

where $\text{cm}(A)$ is the Cayley-Menger determinant of A .

Let $w, z \in \mathbb{R}^n$, and let Q be any $n \times n$ matrix. Using the above formula, we have

$$\det \begin{bmatrix} 1 & z^T \\ w & Q \end{bmatrix} = \det(Q - wz^T).$$

On the other hand, the usual cofactor expansion along the first row gives

$$\det \begin{bmatrix} 1 & z^T \\ w & Q \end{bmatrix} = \det(Q) + \det \begin{bmatrix} 0 & z^T \\ w & Q \end{bmatrix}.$$

Therefore,

$$\det(-wz^T + Q) = \det(Q) + \det \begin{bmatrix} 0 & z^T \\ w & Q \end{bmatrix}.$$

In particular, taking $w = z = 1 \in \mathbb{R}^n$ (the column vector of all ones) and $Q = tA$, we have $\det(-11^T + tA) = \det(tA) + \text{cm}(tA) = t^n \det A + t^{n-1} \text{cm}(A)$. \square

Proof of Theorem 5

In addition to the above ingredients, in order to prove Theorem 5 we will also need the following technical lemma:

Lemma 11 *Fix $v \in \mathbb{R}_\times^n$, and let A be an $n \times n$ Hebbian matrix. If $(-1)^n \text{cm}(A) \leq 0$, then $-vv^T + tA^v$ is not stable for any $t > 0$. In particular, if there exists a $t > 0$ such that $-vv^T + tA^v$ is stable, then $(-1)^n \text{cm}(A) > 0$.*

The proof of this lemma uses the following convexity result:

Lemma 12 *Let M, N be real symmetric $n \times n$ matrices so that M is negative semidefinite (i.e., all eigenvalues are ≤ 0) and N is strictly negative definite (i.e., stable, with all eigenvalues < 0). Then $tM + (1-t)N$ is strictly negative definite (i.e., stable) for all $0 \leq t < 1$.*

Proof M and N satisfy $x^T M x \leq 0$ and $x^T N x < 0$ for all $x \in \mathbb{R}^n$, so we have $x^T (tM + (1-t)N) x < 0$ for all nonzero $x \in \mathbb{R}^n$ if $0 \leq t < 1$. \square

Proof (Proof of Lemma 11) First, some observations. Since A is symmetric, so are A^v and $-vv^T + tA^v$ for any t . Hence, if any principal submatrix of $-vv^T + tA^v$ is unstable then $-vv^T + tA^v$ is unstable (see Corollary 4). Therefore, without loss of generality, we can assume $(-1)^{|\sigma|} \text{cm}(A_\sigma) > 0$ for all proper principal submatrices A_σ , with $|\sigma| < n$ (otherwise, we use this argument on a smallest principal submatrix such that $(-1)^{|\sigma|} \text{cm}(A_\sigma) \leq 0$). By Lemma 9, this implies that A_σ is a nondegenerate square distance matrix for all $|\sigma| < n$, and so we also know by Proposition 3 that $(-1)^{|\sigma|} \det A_\sigma < 0$ and that each A_σ has one positive eigenvalue and all other eigenvalues negative, for all $1 < |\sigma| < n$.

We prove the lemma by contradiction. Suppose there exists a $t_0 > 0$ such that $-vv^T + t_0 A^v$ is stable. Applying Lemma 12 with $M = -vv^T$ and $N = -vv^T + t_0 A^v$, we

have that $-vv^T + (1-t)t_0A^v$ is stable for all $0 \leq t < 1$. It follows that $-vv^T + tA^v$ is stable for all $0 < t \leq t_0$. Now Lemma 4 implies that $(-1)^n \det(-vv^T + tA^v) > 0$ for all $0 < t \leq t_0$. By Lemma 10, this is equivalent to having $(-1)^n(t \det A + \text{cm}(A)) > 0$ for all $0 < t \leq t_0$. By assumption, $(-1)^n \text{cm}(A) \leq 0$, but if $(-1)^n \text{cm}(A) < 0$, then there would exist a small enough $t > 0$ such that $(-1)^n(t \det A + \text{cm}(A)) < 0$, so we can conclude that $\text{cm}(A) = 0$ and $(-1)^n \det A > 0$.

Let $\lambda_1 \leq \dots \leq \lambda_n \leq \lambda_{n+1}$ denote the eigenvalues of the Cayley-Menger matrix $CM(A) = \begin{bmatrix} 0 & 1^T \\ 1 & A \end{bmatrix}$, and observe that A , $A_{[n-1]}$, and $CM(A_{[n-1]})$ are all principal submatrices of $CM(A)$. Since everything is symmetric, Cauchy's interlacing theorem applies. We have seen above that $A_{[n-1]}$ has one positive eigenvalue and all others negative, so by Cauchy's interlacing theorem $\lambda_{n+1} > 0$ and $\lambda_{n-2} < 0$. Because $\text{cm}(A) = \det CM(A) = 0$, $CM(A)$ must have a zero eigenvalue, while $\det A \neq 0$ implies (using Cauchy's interlacing theorem) that it is unique. We thus have two cases.

Case 1: Suppose $\lambda_{n-1} = 0$ and thus $\lambda_n > 0$. Since we assume $(-1)^{n-1} \text{cm}(A_{[n-1]}) > 0$, the $n \times n$ matrix $CM(A_{[n-1]})$ must have an odd number of positive eigenvalues, but by Cauchy's interlacing theorem the top two eigenvalues must be positive, so we have a contradiction.

Case 2: Suppose $\lambda_n = 0$ and thus $\lambda_{n-1} < 0$. Then by Cauchy's interlacing theorem, A has exactly one positive eigenvalue. On the other hand, the fact that $(-1)^n \det A > 0$ implies that A has an even number of positive eigenvalues, which is a contradiction. \square

We can now prove Theorem 5.

Proof (Proof of Theorem 5) We prove $(4) \Rightarrow (3) \Rightarrow (2) \Rightarrow (1) \Rightarrow (4)$.

$(4) \Rightarrow (3) \Rightarrow (2)$ is obvious.

$(2) \Rightarrow (1)$: Suppose there exists a $t > 0$ such that $-vv^T + tA^v$ is stable. Then, by Corollary 4 and Lemma 11, $(-1)^{|\sigma|} \text{cm}(A_\sigma) > 0$ for all principal submatrices A_σ . By Lemma 9 it follows that A is a nondegenerate square distance matrix.

$(1) \Rightarrow (4)$: Suppose A is a nondegenerate square distance matrix. By Lemma 9 we have $(-1)^{|\sigma|} \text{cm}(A_\sigma) > 0$ for all A_σ , while Proposition 3 implies $(-1)^{|\sigma|} \det(A_\sigma) < 0$ for all A_σ with $|\sigma| > 1$. This implies that for $|\sigma| > 1$ we have $-\frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} > 0$ (Corollary 5), and that if $\varepsilon > 0$,

$$(-1)^{|\sigma|} (\varepsilon \det(A_\sigma) + \text{cm}(A_\sigma)) > 0 \Leftrightarrow \varepsilon < -\frac{\text{cm}(A_\sigma)}{\det(A_\sigma)}.$$

Applying now Lemma 10,

$$(-1)^{|\sigma|} \det(-vv^T + \varepsilon A^v)_\sigma > 0 \Leftrightarrow \varepsilon < -\frac{\text{cm}(A_\sigma)}{\det(A_\sigma)}.$$

For $|\sigma| = 1$, we have diagonal entries $A_\sigma = A_\sigma^v = 0$ and $(-vv^T)_\sigma < 0$, so $(-1) \det(-vv^T + \varepsilon A^v)_\sigma > 0$ for all ε . Using Lemma 4, we conclude (assuming $\varepsilon > 0$):

$$-vv^T + \varepsilon A^v \text{ is stable} \Leftrightarrow \varepsilon < \delta,$$

where

$$\delta = \min \left\{ -\frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} \right\}_{\sigma \subseteq [n]} > 0.$$

It remains only to show that $\delta = -\text{cm}(A)/\det(A)$. Note that we can not use Lemma 1 from the Main Text, since this Lemma follows from Proposition 1, and is hence a consequence of Theorem 5.

Because the matrix $-vv^T + \varepsilon A^v$ changes from stable to unstable at $\varepsilon = \delta$, by continuity of the eigenvalues as functions of ε it must be that

$$\det(-vv^T + \delta A^v) = 0.$$

Using Lemma 10 it follows that $\delta \det(A) + \text{cm}(A) = 0$, which implies $\delta = -\text{cm}(A)/\det(A)$. \square

Remarks on the ratio $-\frac{\text{cm}(A)}{\det(A)}$

Remark 1. If A is an $n \times n$ nondegenerate square distance matrix for $n > 1$, then the ratio $-\frac{\text{cm}(A)}{\det(A)}$ has a very nice geometric interpretation:

$$-\frac{\text{cm}(A)}{\det(A)} = \left| \frac{\text{cm}(A)}{\det(A)} \right| = \frac{1}{2\rho^2},$$

where ρ is the radius of the unique sphere circumscribed on the points used to generate A . This is proven in [7, Proposition 9.7.3.7], where it is also shown that $\det(A) \neq 0$ not only if A is a nondegenerate square distance matrix, but also if A is a *degenerate* square distance matrix corresponding to n points in general position in \mathbb{R}^{n-2} . Since $\text{cm}(A)$ vanishes in this case, we see that the ratio $-\frac{\text{cm}(A)}{\det(A)}$ goes smoothly to zero as n points that are initially in general position in \mathbb{R}^{n-1} approach general position on a hyperplane of dimension $n-2$.

Remark 2. The above observations have important implications for the apparent “fine-tuning” that is involved in eliminating spurious cliques by arranging points to be collinear, or coplanar, so that the corresponding principal submatrix A_σ is degenerate (as in Figure 2B). Since $-11^T + \varepsilon A_\sigma$ is only stable for

$$0 < \varepsilon < -\frac{\text{cm}(A_\sigma)}{\det(A_\sigma)} = \frac{1}{2\rho^2},$$

where ρ is the radius of the circumscribed sphere, then by making the points $\{p_i\}_{i \in \sigma}$ corresponding to A_σ *approximately* degenerate, ρ can be made large enough so that $-11^T + \varepsilon A_\sigma$ is unstable – without the fine-tuning required to make A_σ exactly degenerate.

Similarly, exact solutions for k -skeleta of clique complexes, which seem to require S to be a *degenerate* square distance matrix, are also not as fine-tuned as they might first appear. If, in fact, S is a nondegenerate square distance matrix, corresponding to a configuration of n points in \mathbb{R}^{n-1} that *approximately* lies on a k -dimensional plane, the value of $\delta(S_\sigma)$ will be very small for any pattern of size $|\sigma| > k + 1$; one can thus choose ε large enough to ensure that $\text{geom}_\varepsilon(S) = \{\sigma \subset [n] \mid |\sigma| \leq k + 1\}$, as in the case where S is truly degenerate.

Remark 3. It is quite simple to understand the scaling properties of $-\text{cm}(A)/\det(A)$. If A is any $n \times n$ matrix, then $\text{cm}(tA) = t^{n-1}\text{cm}(A)$, while $\det(tA) = t^n \det(A)$, so

$$-\frac{\text{cm}(tA)}{\det(tA)} = \frac{1}{t} \left(-\frac{\text{cm}(A)}{\det(A)} \right),$$

independent of n . If $A_{ij} = \|p_i - p_j\|^2$, for $p_1, \dots, p_n \in \mathbb{R}^{n-1}$, and we scale the position vectors so that $p_i \mapsto tp_i$ for each $i \in [n]$, then $A \mapsto t^2 A$ and we have

$$-\frac{\text{cm}(A)}{\det(A)} \mapsto \frac{1}{t^2} \left(-\frac{\text{cm}(A)}{\det(A)} \right).$$

This is consistent with the fact that the radius of the circumscribed sphere, ρ , scales as $\rho \mapsto t\rho$ in this case (see Remark 1).

Remark 4. Consider an $n \times n$ matrix A satisfying the Hebbian conditions $A_{ij} = A_{ji} \geq 0$ and $A_{ii} = 0$. If n is large, it is computationally intensive to test whether or not A is a nondegenerate square distance matrix using the criteria of Lemma 9, which potentially require computing $\text{cm}(A_\sigma)$ for all $\sigma \subset [n]$.

On the other hand, our results imply that in order to test whether or not a Hebbian matrix A is a nondegenerate square distance matrix it is enough to check the stability of the matrix

$$-11^T + \varepsilon A, \text{ for } \varepsilon = \frac{1}{2} \left| \frac{\text{cm}(A)}{\det(A)} \right|.$$

Here the factor of $1/2$ was chosen somewhat arbitrarily, and can be replaced with any number $0 < c < 1$. For large n , this is a computationally efficient strategy, as it requires checking the eigenvalues of just one matrix.

Remark 5. To use truly binary synapses, we can choose S in the Encoding Rule to be the uniform synaptic strength matrix having $S_{ij} = 1$ for $i \neq j$ and $S_{ii} = 0$ for

all $i \in [n]$. In fact, S is a nondegenerate square distance matrix, and the ratio $\delta(S) = |\text{cm}(S)/\det(S)| = \frac{n}{n-1}$ turns out to have a very simple form. Similarly, any $k \times k$ principal submatrix S_σ , with $|\sigma| = k$, satisfies $\delta(S_\sigma) = \frac{k}{k-1}$. This implies that $\text{geom}_\varepsilon(S)$ is the k -skeleton of the complete simplicial complex on n vertices if $\frac{k+2}{k+1} < \varepsilon < \frac{k+1}{k}$. By the same argument as above, for this choice of S and ε the Encoding Rule yields $\mathcal{C}(W) = X_k(G(\mathcal{P})) = \mathcal{P}$, with W an exact solution for \mathcal{P} . Note that if we choose $0 < \varepsilon \leq 1$, then $\text{geom}_\varepsilon(S) = \text{geom}(S) = 2^{[n]}$, so the resulting $\mathcal{C}(W) \supseteq \mathcal{P}$ for any choice of \mathcal{P} (c.f. [33]).

Details related to generation of PF codes for Figure 1

To produce Figure 1, we generated random k -sparse PF codes with circular place fields, $n = 80$ -100 neurons, and $k = .1n$. For each code, n place field centers were selected uniformly at random from a square box environment of side length 1, and n place field radii were drawn independently from an experimentally observed gamma distribution (Figure 3). We then computed the 2-skeleton for each PF code, with pairwise and triple overlaps of place fields determined from simple geometric considerations. The full PF code was obtained as the Helly completion of the 2-skeleton (see Lemma 2). Finally, to obtain the k -sparse PF code, we restricted the full code to its $(k-1)$ -skeleton, thereby eliminating patterns of size larger than k .

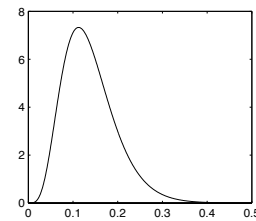


Fig. 3 Gamma distribution used for generating random place field radii; this fits the experimentally-observed mean and variability (see [12, Figure 4B]).

Another exact solution for Figure 2 example

Recall the simplicial complex in Figure 2A. Let S be the symmetric matrix defined by the following equations for $i < j$: $S_{ij} = 1$ if $i = 1$; $S_{24} = S_{35} = 1$; $S_{23} = S_{26} = S_{36} = 3^2$; and $S_{ij} = 5^2$ if $i = 4$ or 5 . (Here we've assigned values corresponding to each

edge in $G(\mathcal{P})$; remaining entries may be chosen arbitrarily, as they play no role.) Note that S is *not* a square distance matrix. Choose $0 < \varepsilon < \delta(S)$, so that $\mathcal{C}(W)$ is given by (3) after applying the Encoding Rule with \mathcal{P} . It is straightforward to check that, among all cliques of $X(G(\mathcal{P}))$, only the desired patterns are encoded. For example, $\{124\} \in \mathcal{C}(W)$ because $S_{\{124\}}$ is a nondegenerate square distance matrix, as the square roots of the entries satisfy all triangle inequalities. In contrast, a triangle inequality is violated for each of $\{123\}$, $\{145\}$, $\{246\}$, and $\{356\}$.

References

1. Amari, S.: Dynamics of pattern formation in lateral-inhibition type neural fields. *Biol Cybern* **27**(2), 77–87 (1977)
2. Amit, D.J.: Modeling brain function. Cambridge University Press, Cambridge (1989). The world of attractor neural networks
3. Andersen, P., Morris, R., Amaral, D., Bliss, T., O’Keefe, J.: The Hippocampus Book. Oxford University Press (2006)
4. Barth, A.L., Poulet, J.F.: Experimental evidence for sparse firing in the neocortex. *Trends Neurosci* **35**(6), 345–355 (2012)
5. Barvinok, A.: A course in convexity, *Graduate Studies in Mathematics*, vol. 54 (2002)
6. Ben-Yishai, R., Bar-Or, R.L., Sompolinsky, H.: Theory of orientation tuning in visual cortex. *Proc Natl Acad Sci U S A* **92**(9), 3844–8 (1995)
7. Berger, M.: Geometry. I. Universitext. Springer-Verlag, Berlin (1994). Translated from the 1977 French original by M. Cole and S. Levy, Corrected reprint of the 1987 translation
8. Blumenthal, L.M.: Theory and applications of distance geometry. Oxford, at the Clarendon Press (1953)
9. Bott, R., Tu, L.W.: Differential forms in algebraic topology. Springer-Verlag, New York (1982)
10. Bressloff, P.C.: Spatiotemporal dynamics of continuum neural fields. *J. Phys. A* **45**(3) (2012)
11. Curto, C., Degeratu, A., Itskov, V.: Flexible memory networks. *Bulletin of Mathematical Biology* **74**(3), 590–614 (2012)
12. Curto, C., Itskov, V.: Cell groups reveal structure of stimulus space. *PLoS Comput Biol* **4**(10) (2008)
13. Dayan, P., Abbott, L.F.: Theoretical neuroscience. MIT Press, Cambridge, MA (2001)
14. Deza, M.M., Laurent, M.: Geometry of cuts and metrics, *Algorithms and Combinatorics*, vol. 15. Springer-Verlag, Berlin (1997)
15. Ermentrout, G., Terman, D.: Mathematical Foundations of Neuroscience. Springer (2010)
16. Hahnloser, R.H., Seung, H.S., Slotine, J.J.: Permitted and forbidden sets in symmetric threshold-linear networks. *Neural Comput* **15**(3), 621–638 (2003)
17. Hertz, J., Krogh, A., Palmer, R.G.: Introduction to the theory of neural computation. Addison-Wesley, Redwood City, CA (1991)
18. Hillar, C., Tran, N., Koepsell, K.: Robust exponential binary pattern storage in little-hopfield networks. arXiv:1206.2081 [q-bio.NC] (2012)
19. Hopfield, J.J.: Neural networks and physical systems with emergent collective computational abilities. *Proc. Natl. Acad. Sci.* **79**(8), 2554–2558 (1982)
20. Horn, R., Johnson, C.: Matrix Analysis. Cambridge University Press (1985)
21. Hromádka, T., Deweese, M.R., Zador, A.M.: Sparse representation of sounds in the unanesthetized auditory cortex. *PLoS Biol* **6**(1) (2008)
22. Itskov, V., Hansel, D., Tsodyks, M.: Short-term facilitation may stabilize parametric working memory trace. *Frontiers in Computational Neuroscience* **5**, 1–19 (2011)
23. McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., Moser, M.B.: Path integration and the neural basis of the ‘cognitive map’. *Nat Rev Neurosci* **7**(8), 663–78 (2006)
24. Muller, R.: A quarter of a century of place cells. *Neuron* **17**(5), 813–822 (1996)
25. Niskanen, S., Ostergard, P.: Cliquer - routines for clique searching (2010). Available at <http://users.tkk.fi/pat/cliquer.html>
26. O’Keefe, J.: Place units in the hippocampus of the freely moving rat. *Exp. Neurol.* **51**, 78–109 (1976)
27. O’Keefe, J., Nadel, L.: The Hippocampus as a Cognitive Map. Clarendon Press, Oxford, UK (1978)
28. Oxley, J.: Matroid theory, *Oxford Graduate Texts in Mathematics*, vol. 21, second edn. Oxford University Press, Oxford (2011)
29. Petersen, C.C.H., Malenka, R.C., Nicoll, R.A., Hopfield, J.J.: All-or-none potentiation at CA3-CA1 synapses. *PNAS* **95**, 4732–4737 (1998)
30. Schoenberg, I.J.: Remarks to Maurice Fréchet’s article “Sur la définition axiomatique d’une classe d’espace distanciés vectoriellement applicable sur l’espace de Hilbert”. *Ann. of Math. (2)* **36**(3), 724–732 (1935). DOI 10.2307/1968654. URL <http://dx.doi.org/10.2307/1968654>
31. Shriki, O., Hansel, D., Sompolinsky, H.: Rate models for conductance-based cortical neuronal networks. *Neural Comput* **15**(8), 1809–1841 (2003)
32. Ulanovsky, N.: Neuroscience: how is three-dimensional space encoded in the brain? *Curr Biol* **21**, 886–888 (2011)
33. Xie, X., Hahnloser, R.H., Seung, H.S.: Selectively grouping neurons in recurrent networks of lateral inhibition. *Neural Comput* **14**, 2627–46 (2002)